2013

Influence of management and precipitation on carbon fluxes in Great Plains grasslands

Matthew Rigge
U.S. Geological Survey Earth Resources Observation and Science Center, mrigge@usgs.gov

Bruce K. Wylie
USGS EROS, wylie@usgs.gov

Li Zhang
Chinese Academy of Sciences, Beijing

Stephen P. Boyte
Stinger Ghaffarian Technologies, Inc.

Ecological Indicators 34 (2013) 590–599

Contents lists available at SciVerse ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original article

Influence of management and precipitation on carbon fluxes in great plains grasslands☆

Matthew Rigge[a,*], Bruce Wylie[b], Li Zhang[c], Stephen P. Boyte[d]

[a] Arctic Slope Regional Corporation Research & Technology Solutions, Contractor to U.S. Geological Survey Earth Resources Observation and Science Center, Sioux Falls, SD 57198, USA
[b] U.S. Geological Survey Earth Resources Observation and Science Center, Sioux Falls, SD 57198, USA
[c] Key Laboratory of Digital Earth, Center for Earth Observation and Digital Earth, Chinese Academy of Sciences, Beijing 100094, China
[d] Stinger Ghaffarian Technologies, Inc. Contractor to the U.S. Geological Survey Earth Resources Observation and Science Center, Sioux Falls, SD 57198, USA

ARTICLE INFO

Article history:
Received 5 December 2012
Received in revised form 24 June 2013
Accepted 27 June 2013

Keywords:
Grasslands
Carbon balance
Net ecosystem productivity
Ecosystem performance
Grazing
Phenology

ABSTRACT

Suitable management and sufficient precipitation on grasslands can provide carbon sinks. The net carbon accumulation of a site from the atmosphere, modeled as the Net Ecosystem Productivity (NEP), is a useful means to gauge carbon balance. Previous research has developed methods to integrate flux tower data with satellite biophysical datasets to estimate NEP across large regions. A related method uses the Ecosystem Performance Anomaly (EPA) as a satellite-derived indicator of disturbance intensity (e.g., livestock stocking rate, fire, and insect damage). To better understand the interactions among management, climate, and carbon dynamics, we evaluated the relationship between EPA and NEP data at the 250 m scale for grasslands in the Central Great Plains, USA (ranging from semi-arid to mesic). We also used weekly estimates of NEP to evaluate the phenology of carbon dynamics, classified by EPA (i.e., by level of disturbance impact). Results show that the cumulative carbon balance over these grasslands from 2000 to 2008 was a weak net sink of 13.7 $g\,C\,m^{-2}\,yr^{-1}$. Overall, NEP increased with precipitation ($R^2 = 0.39$, $P < 0.05$) from west to east. Disturbance influenced NEP phenology; however, climate and biophysical conditions were usually more important. The NEP response to disturbance varies by ecoregion, and more generally by grassland type, where the shortgrass prairie NEP is most sensitive to disturbance, the mixed-grass prairie displays a moderate response, and tallgrass prairie is the least impacted by disturbance (as measured by EPA). Sustainable management practices in the tallgrass and mixed-grass prairie may potentially induce a period of average net carbon sink until a new equilibrium soil organic carbon is achieved. In the shortgrass prairie, management should be considered sustainable if carbon stocks are simply maintained. The consideration of site carbon balance adds to the already difficult task of managing grasslands appropriately to site conditions. Results clarify the seasonal and interannual dynamics of NEP, specifically the influence of disturbance and moisture availability.

1. Introduction

Grasslands can be a carbon sink with site-appropriate management (i.e., stocking rates) (Owensby et al., 2006; Svejcar et al., 2008; Zhu et al., 2011) and adequate precipitation. Carbon balance is often assessed with the Net Ecosystem Productivity (NEP). NEP is defined as CO_2 uptake by photosynthesis minus CO_2 lost by ecosystem respiration, and represents the net carbon accumulation over a given time interval (Randerson et al., 2002; Chapin et al., 2006). Positive NEP values represent a net carbon uptake by the ecosystem from the atmosphere, and negative values occur when ecosystems release carbon to the atmosphere (Zhang et al., 2010). NEP does not consider lateral flows of carbon (e.g., leaching loss and removal [culling] of herbivores) (Chapin et al., 2006). Carbon removed by grazing is mostly returned through excreta, with only a small fraction exported through the culling of livestock (Soussana et al., 2004). Harvesting biomass, grazing, and fires are additional pathways in which carbon could be removed from a site (Zhu et al., 2011).

Grasslands in the central and northern Great Plains tend to have a long-term cumulative carbon balance near zero (i.e., equilibrium) (Haferkamp and MacNeil, 2004; Owensby et al., 2006; Wylie et al., 2007; Zhang et al., 2010; Chimner and Welker, 2011) or slightly positive (i.e., sink) (Frank and Karn, 2003; Zhang et al., 2011). Root turnover in grassland soils constitutes the largest input to soil

☆ Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

* Corresponding author at: 47914 252nd St., Sioux Falls, SD 57198, USA. Tel.: +1 605 594 2894.
E-mail address: mrigge@usgs.gov (M. Rigge).

1470-160X/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecolind.2013.06.028

organic carbon (SOC), the below-ground C pool, due to the high concentration of lignin and polyphenols, which are resistant to degradation (Soussana et al., 2004). Decomposition of plant and animal residue and deposition by rhizomes also comprise major pathways of SOC deposition, and are directly related to NEP. Precipitation deficits and interannual variability often limit NEP, causing grasslands to become a net carbon source during drought years (Meyers, 2001; Zhang et al., 2010). Net ecosystem exchange in the northern Great Plains was reported to vary widely (spatio-temporally) from −537 to 610 g C m^{-2} yr^{-1} (Gilmanov et al., 2005).

Improved understanding of grassland carbon fluxes is needed to determine their potential role in mitigating (or contributing to) increasing atmospheric CO_2 concentrations and global change (Gilmanov et al., 2005) and the influence of management on ecosystem carbon cycling and equilibrium SOC (Owensby et al., 2006; Svejcar et al., 2008). Management (e.g., grazing intensity) can have a strong impact on grassland carbon balance (Soussana et al., 2004; Owensby et al., 2006; Svejcar et al., 2008; Zhu et al., 2011). Grazing affects ecosystem carbon flux by influencing species composition and the rate of carbon incorporation into soil, while grazing exclusion allows litter to accumulate and often reduces the rate of carbon assimilation (Milchunas and Lauenroth, 1993; Reeder and Schuman, 2002; Haferkamp and MacNeil, 2004). Though grazing often reduces a substantial portion of aboveground live biomass (Haferkamp and MacNeil, 2004; Derner et al., 2006), most grassland carbon is belowground (Schuman et al., 1999), thus NEP does not have a consistently strong correlation with aboveground live biomass. The effect of grazing intensity on carbon balance is non-linear and varies by ecosystem (Owensby et al., 2006).

Equilibrium SOC levels are only altered with management and environmental changes. Schuman et al. (2002), for example, estimated that implementing proper grazing management could increase carbon sinks on U.S. grasslands by 10–30 g C m^{-2} $year^{-1}$, for a period of time until a new equilibrium SOC is achieved. Gebhart et al. (1994) demonstrated that these changes can be rapid; with significant increases to SOC within 5 years of altered management practices (e.g., cropland to grassland conversion or change in livestock management practices), though decades may be required to reach a new equilibrium (Soussana et al., 2004). Minimal increases to SOC would be expected beyond this point (Schuman et al., 2002).

Land managers have the difficult decision of setting a stocking rate appropriate to site conditions (Schuman et al., 1999), which is even more difficult with the consideration of carbon fluxes. One tool available to assist rangeland managers in setting a sustainable stocking rate is the Ecosystem Performance Anomaly (EPA) (Wylie et al., 2008; Rigge et al., 2013). The EPA is calculated using ecosystem models and satellite data to describe the departure of annual biomass production from the level expected by annual weather conditions and site potential (driven by soils, aspect, slope, climate, etc.) at each pixel, a method that has been successfully applied to several ecosystems and validated by a variety of field data (Wylie et al., 2008; Rigge et al., 2013). By simultaneously monitoring the NEP and EPA of a site (i.e., measuring the carbon flux and proxy of disturbance intensity/stocking rate) we can more fully describe the complex connection between the two. Moreover, this technique may guide recommendations for improving the suitability of grassland management practices that enhance carbon sequestration in the ecoregions of the Great Plains.

1.1. Objectives

Our objectives were to assess the interactions among NEP (Zhang et al., 2010), EPA (Wylie et al., 2008), and precipitation for grasslands in the Greater Platte River Basin. This was accomplished using three techniques. First, we determined the quantity of precipitation needed to induce a carbon sink (i.e., NEP ≥ 0 g C m^{-2} yr^{-1}) at each pixel. Second, the temporal correlation between EPA and NEP was calculated at each pixel. Finally, we used weekly NEP data to develop average NEP phenologies for grassland types and ecoregions (Omernik, 1987), which were subsequently stratified by EPA class (i.e., level of grazing and/or disturbance impact), to better understand the connections between management, climate, and carbon dynamics across a range of environmental conditions.

2. Materials and methods

2.1. Study area

We evaluated grasslands, using the areas classified by the 2006 National Land Cover Dataset (NLCD) (Fry et al., 2011) as herbaceous and hay/pasture, in the Greater Platte River Basin. This Basin includes the Platte River watershed in addition to the ecologically similar Republican and Niobrara River watersheds in the central and northern Great Plains, USA (Fig. 1C). Omernik Level III ecoregions were used for comparison and reference in our analysis (Omernik, 1987). Our study area included the grassland portions of the High Plains, Nebraska Sand Hills, Northwestern Great Plains, Northwestern Glaciated Plains, Southwestern Tablelands, Central Great Plains, Western Corn Belt Plains, and Flint Hills ecoregions within the Greater Platte River Basin. Ecoregions ranged from 21% grassland cover in the Western Corn Belt Plains to 83% in the Northwest Great Plains, with a study area average of 58% grassland cover. The portions of the Southern Rockies and Wyoming Basin ecoregions that were present within the Greater Platte hydrologic basin were excluded from this study due to their ecological dissimilarity (i.e., dominance of woody species cover and/or mountainous topography).

Evaluated grassland ecosystems range from mesic tallgrass prairie in the east to semi-arid shortgrass prairie in the west. We defined the shortgrass prairie as the High Plains and Southwestern Tablelands ecoregions; mixed-grass as the Nebraska Sand Hills, Northwestern Great Plains, and Northwestern Glaciated Plains ecoregions; and tallgrass as the Central Great Plains, Western Corn Belt Plains, and Flint Hills ecoregions (Sims et al., 1978; Omernik, 1987; Table 1; Fig. 1C). Shortgrass, mixed-grass, and tallgrass types occupied 41%, 39%, and 20% of total grassland areas, respectively. We recognize that this grouping of ecoregions into grassland types does not exactly match the spatial distribution of the defined grassland types. For example, tallgrass prairie occurs in parts of the Nebraska Sand Hills ecoregion, and mixed-grass prairie occurs in parts of the Central Great Plains ecoregion. However, our defined grassland types correspond closely with those described by Johnson and Larson (2007).

The tallgrass prairie is dominated by big bluestem (*Andropogon gerardi* Vitman), switchgrass (*Panicum virgatum* L.), and Indiangrass (*Sorghastrum nutans* L.), with some areas invaded by Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss). The mixed-grass prairie includes sand bluestem (*Andropogon hallii* Hack.), switchgrass, porcupine grass (*Hesperostipa spartea* Trin.), western wheatgrass (*Pascopyrum smithii* Rybd.), and junegrass (*Koeleria pyramidata* Lam). Finally, the shortgrass prairie is dominated by blue grama (*Bouteloua gracilis* Kunth) and buffalo grass (*Bouteloua dactyloides* Nutt.) (Sims et al., 1978; Zhang et al., 2010). Total biomass production, precipitation, and the percentage of total biomass production contributed by C_4 plants all increase from northwest to southeast across the study area (Sims et al., 1978; Tieszen et al., 1997). Average precipitation, based on 30-year average Parameter-Elevation Regressions on Independent Slopes Model (PRISM) weather data (PRISM Climate Group, Oregon State University, http://www.prismclimate.org) ranged from approximately 200 mm in the west to 600 mm in the east.

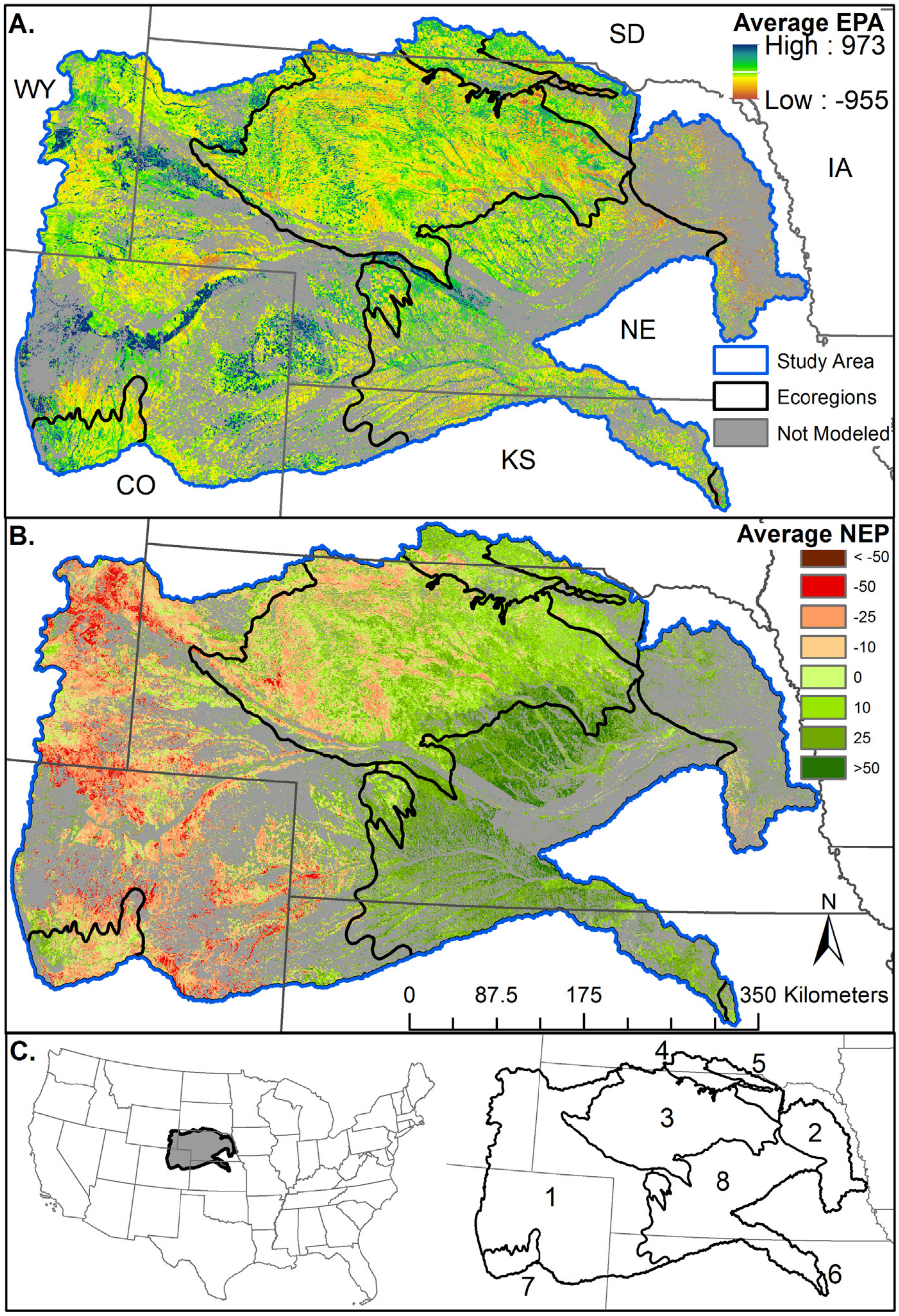

Fig. 1. (A) 2000–2008 mean Ecosystem Performance Anomaly (EPA) for grasslands in the Greater Platte River Basin, where values greater than 100 represent significant (90% confidence) overperformance and values under −100 represent significant underperformance, (B) 2000–2008 mean Net Ecosystem Productivity (NEP; $g\,C\,m^{-2}\,yr^{-1}$), where carbon uptake by plants is represented by a positive NEP and release to the atmosphere is a negative value, and (C) location of the study area within the United States and location of ecoregions (numbered) within the study area. Ecoregion codes are: (1) High Plains, (2) Western Corn Belt Plains, (3) Nebraska Sand Hills, (4) Northwestern Great Plains, (5) Northwestern Glaciated Plains, (6) Flint Hills, (7) Southwestern Tablelands, and (8) Central Great Plains. EPA and NEP were not modeled in non-grassland areas.

Table 1
2000–2008 mean Ecosystem Performance Anomaly (EPA), cumulative Net Ecosystem Productivity (NEP; $g\,C\,m^{-2}\,yr^{-1}$) across the entire study period, EPA to NEP correlation[a] by ecoregion, and temporal correlation[b] between precipitation and NEP in grasslands of the Greater Platte River Basin. Spatio-temporal SE contained in parenthesis.

Ecoregion	EPA	NEP	EPA:NEP[a]	Precipitation:NEP[b]
High Plains	1.0 (1.2)	−3.1 (3.3)	−0.01	0.65
Western Corn Belt Plains	−0.4 (10.1)	20.8 (2.6)	0.11	0.14
Nebraska Sand Hills	−18.3 (1.0)	14.6 (8.1)	−0.05	0.84
Northwestern Great Plains	−16.3 (4.2)	15.6 (34.0)	−0.06	0.68
Northwestern Glaciated Plains	−3.9 (6.6)	17.7 (9.0)	−0.04	0.14
Flint Hills	12.2 (3.2)	26.2 (18.1)	0.16	0.52
Southwest Tablelands	0.8 (3.0)	−3.7 (6.6)	0.29	0.35
Central Great Plains	−5.6 (2.0)	42.3 (2.9)	0.03	0.67
Study Area Average	−10.1 (0.7)	13.7 (2.2)	0.02	0.84

[a] Temporal correlation coefficient (r) between yearly EPA and NEP in each pixel (from Fig. 4), averaged by ecoregion.
[b] Temporal correlation coefficient (r) between ecoregion averaged annual precipitation and ecoregion averaged NEP.

2.2. Data

Our approach to model EPA consisted of three steps (after Wylie et al., 2008; Rigge et al., 2013): (1) determine the actual performance of each pixel, each year, with weekly Normalized Difference Vegetation Index (NDVI) images averaged over the growing season (GSN), (2) define the expected ecosystem performance (EEP) at each pixel, each year, given yearly weather conditions and site potential, and assuming an absence of disturbance, and (3) assess EPA as the GSN departure from EEP.

2.2.1. Ecosystem Performance Anomalies (EPA)

To determine actual performance, we used 250 m expedited Moderate Resolution Imaging Spectroradiometer (eMODIS) Normalized Difference Vegetation Index (NDVI) imagery, temporally smoothed (Swets et al., 2000) into 7-day composites (Jenkerson et al., 2010) for 2000–2008, in the Albers Equal Area projection. The NDVI composites were averaged over the course of a growing season (defined as 1 April to 30 September) to produce Growing Season NDVI (GSN), a proxy of actual yearly ecosystem performance (Wylie et al., 2008) that is spatially and temporally consistent. Remotely sensed vegetation indices such as the NDVI are strongly related to CO_2 flux, plant biomass, total ecosystem respiration, and Leaf Area Index (LAI) (Frank and Karn, 2003; Gilmanov et al., 2005), while GSN has been strongly correlated with Soil Survey Geographic (SSURGO) annual productivity for grasslands (Gu et al., 2013). GSN values include the effects of disturbances such as fire and insect damage, grazing, site potential, and yearly weather conditions (Wylie et al., 2008; Rigge et al., 2013).

Site potential represents the modeled 2000–2008 average GSN at each pixel. To calculate site potential, we used rule-based piecewise regression trees (using Cubist® software: http://www.rulequest.com/) to model the nonlinear response of long-term productivity to a variety of factors including long-term (1971–2000) climate (precipitation and temperature [minimum and maximum]) (PRISM), land form, elevation, aspect, slope, compound terrain index, soil organic carbon (SSURGO), range productivity from a normal year (SSURGO), environmental site potential (*LANDFIRE*), ecoregions, and Major Land Resource Areas (MLRA) (Wylie et al., 2008). The Cubist® model partitions data into nodes based on a series of rules, at which multiple linear regression models are established. We used the committee (of 5) model option in Cubist®, with the first model focusing on dominant relationships and other models generally evaluating outliers; all models were averaged for the final product. EEP values were the estimated GSN for individual years at each pixel. A separate Cubist® rule-based piecewise regression model was used to calculate yearly EEP from site potential and yearly weather conditions (i.e., seasonal precipitation, maximum temperature, and minimum temperature composites [PRISM]) at each pixel (Rigge et al., 2013). Site potential was incorporated into the EEP model due to linkages between these datasets (i.e., sites with poor conditions from vegetative growth [low site potential] will also have a lower EEP). The site potential represents the long-term average expected productivity for each pixel, while the EEP fluctuates with yearly weather conditions. Areas of known disturbances, such as those burned in the last 25 years (Monitoring Trends in Burn Severity [MTBS]), were excluded from the development of site potential and EEP models, while grazed sites are included.

EPA values represent the divergence between actual and expected ecosystem performance (Wylie et al., 2008). EPA was calculated as the GSN minus EEP in each pixel, each year. Our approach assumes a uniform effect of weather on GSN and EEP, making EPA independent of spatial and temporal variations in weather (Rigge et al., 2013). The units of EPA are confidence limits, with an EPA of ±100 set to correspond with the 90% confidence limits of the EEP to yearly GSN relationship. Setting a constant confidence limit standardizes the sensitivity of the EPA to perturbation. The confidence limits separate the EPA into categories; pixels with an EPA significantly lower than expected are referred to as underperforming, while pixels with an EPA significantly higher than expected are referred to as overperforming. GSN values within the confidence limits are referred to as having a normal performing EPA. Since the EEP does not consider disturbance (e.g., fires, insect damage, etc.), any disturbance that occurred was mapped as a departure from expected conditions, namely as underperforming EPA. Therefore, deviations in grazing intensity (i.e., animal unit months [AUM] ha^{-1}) of a pixel from average conditions would in theory cause the GSN to be different than the EEP, resulting in an EPA value not equal to zero. Grassland species composition and diversity data are not available at a regional scale, so our model does not consider the generally positive influence of species diversity on grassland productivity (Tilman et al., 1997). We assume that diversity will generally be positively correlated with EPA. The EPA approach has been successfully used in a variety of ecosystems and validated be field observations (Wylie et al., 2008; Rigge et al., 2013).

2.2.2. Net Ecosystem Productivity (NEP)

The same 250 m, 7-day eMODIS NDVI composites used to generate EPA were used for the development of the NEP model (Zhang et al., 2011). We used gap-filled (Gilmanov et al., 2005) NEP data from 14 flux tower sites located in grasslands throughout the Great Plains (public.ornl.gov/ameriflux/). Raw flux tower data were acquired from the AmeriFlux (using eddy-covariance measurements [Law, 2007]) and Rangeflux networks (using the Bowen ratio energy balance method [Svejcar et al., 1997]). The 1971–2000 climate data (precipitation and temperature [minimum and maximum]) data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center. Photosynthetically active radiation (PAR) was acquired from the NOAA National Environmental Satellite, Data and Information Service (NESDIS; http://www.atmos.umd.edu/,srb/gcip).The NDVI composites, phenological metrics (e.g., start of season and maximum NDVI), 1971–2000 climate data, PAR, soils data, and soil water holding capacity were used as inputs into the rule-based piecewise regression tree (Cubist®) NEP model (Zhang et al., 2010). This model operated at 7-day time intervals that used remotely sensed data as a co-variable to extrapolate NEP measured by flux towers across the landscape for 2000–2008 (Wylie et al., 2007; Zhang et al., 2010, 2011). The model produced NEP estimates across the entire Great Plains, which was subsequently clipped to our study area. Doing so allows the NEP model to incorporate pertinent data from flux tower sites outside of the study area boundary. The NEP model was reported to estimate NEP across large regions with a low degree of error (Wylie et al., 2007; Zhang et al., 2010, 2011).

2.3. Data analysis

2.3.1. Precipitation and NEP relationship

The *x*-intercept of the temporal relationship between 2000 and 2008 mean annual precipitation and 2000–2008 average NEP for each pixel was calculated using simple least-squares linear regression ($n = 9$ at each pixel) (Fig. 2). The *x*-intercept represents the amount of precipitation (predicted by the linear model independently developed in each pixel) required to achieve a NEP $\geq 0\ g\ C\ m^{-2}\ yr^{-1}$. This value was then subtracted from the 2000 to 2008 mean annual precipitation at each pixel and the resulting product was defined as the Precipitation Differential (PD). Areas with positive PD values indicate that average precipitation is sufficient to maintain a carbon sink, while areas with negative PD values

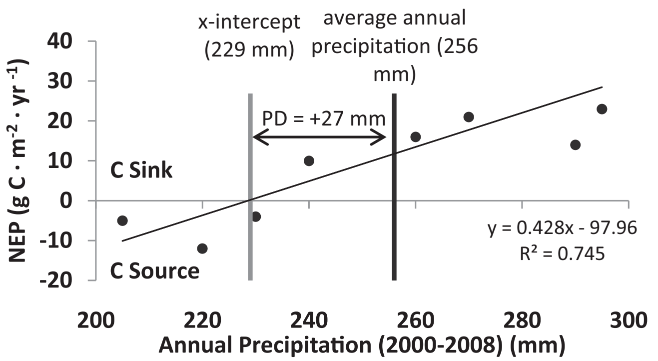

Fig. 2. Example (hypothetical) of Precipitation Differential (PD) calculation at each pixel. First, the *x*-intercept of the annual precipitation to NEP (i.e., carbon flux) regression is calculated independently at each pixel (in this example, 229 mm). This *x*-intercept value is equal to the average quantity of annual precipitation required to induce an NEP $\geq$ 0 g C m^{-2} yr^{-1}. Next, the average annual precipitation (of the 2000–2008 period) is calculated at each pixel (in this example, 256 mm). Finally, the *x*-intercept is subtracted from the average annual precipitation (i.e., 256–229 mm) to yield the PD (equal to +27 mm in this example).

would need greater than average precipitation to produce a carbon sink (Fig. 2). The resulting data help to clarify the spatial patterns in the relationship between precipitation and NEP, and the likelihood of achieving a positive/negative NEP. Additionally, yearly precipitation and yearly NEP were averaged in each ecoregion, and simple linear regressions (n = 9 for each ecoregion) were used to plot the correlation between the two.

2.3.2. EPA and NEP correlation

We calculated the temporal linear correlation coefficient (r) between yearly EPA and yearly NEP (as the dependent variable) (n = 9) for 2000–2008 in all evaluated pixels. These correlation data enable the spatial examination of disturbance impacts on NEP (i.e., the magnitude and direction of the EPA to NEP relationship).

2.3.3. NEP phenology by EPA class

We averaged the yearly temporal profile of NEP (weekly composites) in each pixel across the years 2000–2008 for each of the eight ecoregions. The average sample size by ecoregion was nearly 300,000 points, with a minimum of 6500 points. By averaging the NEP phenology of each pixel across the 9-year study period, the effect of interannual variability is dampened, providing a good estimate of expected NEP phenology by ecoregion. The average NEP phenology in each ecoregion was subsequently grouped by EPA class (n = 3; underperformance, normal performance, and overperformance) to generate 24 unique phenologies, in addition to the overall study area average NEP phenology for each EPA class. These results were used to evaluate the impact of disturbance on the NEP of the evaluated ecoregions. Additionally, we used data pooled across ecoregions to average the yearly temporal profile of NEP in shortgrass, mixed-grass, and tall grass prairies, using the previously described definitions of each. The average sample size in each grassland type was nearly 800,000 points, with a minimum of 480,000 points. In these NEP phenologies the "week of year" labeled zero begins on 1 January, and observations occur on a weekly interval but the units are g C m^{-2} day^{-1}. Finally, we determined the 2000–2008 average yearly cumulative NEP for each EPA class in all ecoregions. A two-sample t-test was used to determine significant (P < 0.05) differences in cumulative NEP among the EPA classes. The 9-year study period includes a wide range of weather conditions, therefore the carbon flux phenologies represent the response to disturbance in an average year.

3. Results and discussion

3.1. Net ecosystem productivity by ecoregion

The cumulative carbon balance over evaluated grasslands from 2000 to 2008 was a weak net sink of 13.7 g C m^{-2} yr^{-1} (Table 1; Fig. 1B) corroborating with Zhu et al. (2011) though our study period contained several major droughts that could greatly reduce carbon assimilation (Zhang et al., 2010; Zhu et al., 2011) in addition to wet years. Caution should be used, however, in interpreting this finding as a consistent pattern due to the timing of droughts (Svejcar et al., 2008), the large interannual variation in cumulative carbon balance (S.E. equal to 3.97 g C m^{-2} yr^{-1}), and the large geographical variation in NEP (Fig. 1). Previous work in the region by Zhang et al. (2010) found that the northern Great Plains from 2000 to 2007 was a weak carbon source at −15 g C m^{-2} yr^{-1}; however, their study area excluded the extensive area of strong net carbon sinks in the Central Great Plains, Sand Hills, and Flint Hills ecoregions. Variability of NEP across ecoregions (Table 1) was significant, comparable to the previously reported interannual variability of NEP in grasslands (Meyers, 2001; Zhang et al., 2010).

NEP increased with precipitation (R^2 = 0.42, P < 0.05) from west to east (Fig. 1B), but was also influenced by soil composition (clay content, organic matter, and water holding capacity) (Zhang et al., 2007), decomposition rates, disturbance, and growing season length (Zhang et al., 2011). Accordingly, NEP tended to be greatest in the southeast, and lowest in the northwest. Individual ecoregions ranged from a weak cumulative carbon source (High Plains) to a strong sink (Central Great Plains) (Table 1), suggesting that soil carbon is more stable in the east. Tallgrass prairie in Texas was reported to have an average NEP of 252 g C m^{-2} yr^{-1} (Svejcar et al., 2008), while our highest per pixel 2000–2008 average rates were only 120 g C m^{-2} yr^{-1} in the Central Great Plains ecoregion (Fig. 1B). The lowest average NEP levels were sources of −77 g C m^{-2} yr^{-1} in the southwestern portion of the High Plains ecoregion (Fig. 1B). The Northwestern Glaciated Plains and Northwestern Great Plains ecoregions were strong carbon sinks (Table 1), a result previously reported by Zhang et al. (2010). Overall, our NEP estimates by ecoregion were similar to those of Zhang et al. (2010), though averaging over the 9-year study period produced values nearer to zero in the current study.

3.2. Precipitation to NEP relationship

As previously discussed, a PD of zero or greater suggests that average precipitation is sufficient to generate a carbon sink. Areas with a positive PD (Fig. 3) are typically a carbon sink (82.3% of cases) while areas with a negative PD are less likely to be such (41.0% of cases; Fig. 1B). The major exception to this pattern occurs in the southeastern portion of the Sand Hills and the adjacent portion of the Central Great Plains with a negative PD (Fig. 3) and positive NEP (i.e., carbon sink) (Fig. 1B). If not for this region, areas with a negative PD would be even less likely to be carbon sinks. This pattern may be related to the nonlinear relationship between precipitation and SOC; where, in the 0–10 cm depth, precipitation above 440 mm does not increase SOC, and may actually decrease it (Derner and Schuman, 2007). Moreover, no flux tower data were available in the Sand Hills for the NEP model.

Areas with lower precipitation tend to have stronger precipitation to NEP correlations while regions with higher average precipitation tend to have a higher x-intercept (of the annual precipitation to NEP relationship) (R^2 = 0.22, P < 0.05). These findings infer that plant communities in drier areas need less water to achieve a carbon sink (i.e., NEP $\geq$ 0 g C m^{-2} yr^{-1}), likely due to more efficient water usage, more conservative growth strategies, and lower moisture facilitation of soil respiration in drier

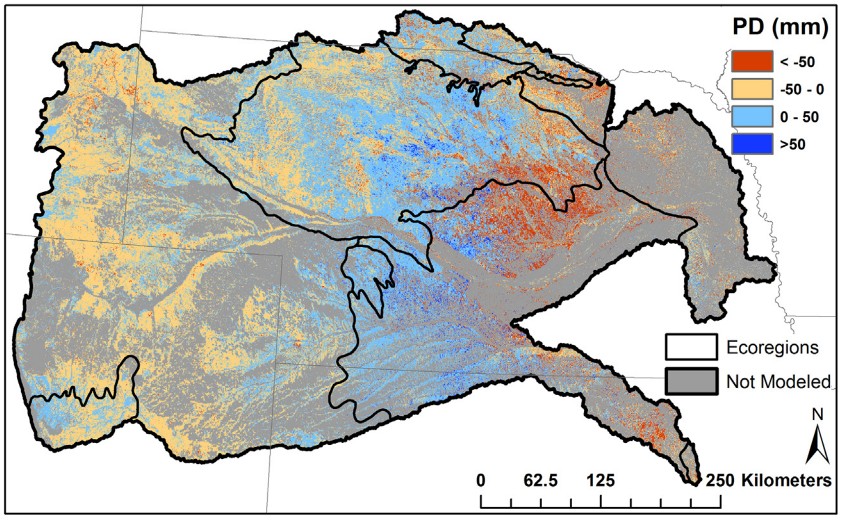

Fig. 3. *x*-Intercept of the temporal relationship between 2000–2008 mean annual precipitation and 2000–2008 mean Net Ecosystem Productivity (NEP) in each pixel, minus 2000–2008 mean annual precipitation, defined as Precipitation Differential (PD). Positive PD values indicate that mean precipitation is greater than the *x*-intercept (of the precipitation:NEP relationship), and that growing conditions usually result in a C sink (see Fig. 2 for an example of PD calculation). Refer to Fig. 1C for ecoregion labels.

areas. Conversely, precipitation is weakly related to PD ($R^2 = 0.05$), because the spatial pattern of PD somewhat diverges from that precipitation (Fig. 3). The concentration of strongly negative PD values in the east-central portion of the study area may be associated with soils near their SOC equilibrium; hence they are resistant to additional C sequestration, needing a well-above average annual precipitation to do so. PD can describe areas in which managing for a carbon sink are most difficult (i.e., it would be difficult to induce [by management alone] a carbon sink in areas with a negative PD and negative NEP). Similarly, we can infer that areas with both a positive NEP and positive PD would have relative carbon stability and would likely require the combination of a drought and heavy grazing to induce a negative NEP, making these sites potentially attractive to biofuels production and carbon sequestration opportunities (Zhu et al., 2011). These sites possess (1) a consistent carbon sink (i.e., positive average NEP) and (2) moisture levels adequate for carbon maintenance (i.e., positive PD), providing environmental conditions that should be able to support sustainable grassland cellulosic biofuels without depleting SOC (Gu et al., 2012).

Annual precipitation and NEP were averaged by ecoregion in each study year, and the resulting values were regressed against each other. As previously discussed, NEP tends to increase with precipitation (Fig. 1B; Table 1), a pattern strongly evident in shortgrass and mixed-grass prairies of the High Plains, Sand Hills, Northwestern Great Plains, and Central Great Plains (Table 1). However, in the tallgrass prairie of the Western Corn Belt Plains, Northwestern Glaciated Plains, and Flint Hills ecoregions, the linkage between yearly precipitation and NEP tends to be weaker. These near horizontal (or insignificant) relationships indicate that NEP tends to be less sensitive to precipitation at higher levels (of precipitation).

3.3. Impacts of disturbance on NEP

3.3.1. EPA and NEP correlation

Grazing is prolific across study area grasslands (Owensby et al., 2006), and is generally thought to reduce ecosystem NEP (Owensby et al., 2006; Svejcar et al., 2008) and EPA (Rigge et al., 2013); therefore, a positive correlation between EPA and NEP would be expected. The overall per pixel spatial correlation between EPA and NEP followed this pattern, with a weak positive association ($r = 0.02$) (Table 1; Fig. 4), though individual pixels and ecoregions demonstrated stronger correlations. The average EPA value of −10.1 echoes these findings, suggesting that disturbances and grazing (which is not considered in the EPA model), on average, resulted in a lower actual grassland productivity (i.e., GSN) than expected by our model (i.e., EEP) (Table 1; Fig. 1A). Conversely, negative correlations between EPA and NEP (i.e., light to moderate disturbance increases NEP) have been reported in the shortgrass and mixed-grass prairies (Milchunas and Lauenroth, 1993; Chimner and Welker, 2011), largely agreeing with our results (Table 1). Eliminating grazing is not likely to increase SOC, and in fact can reduce carbon storage because moderate grazing can stimulate plant growth (Reeder and Schuman, 2002; Schuman et al., 2002), even though grazing often reduces a substantial portion of aboveground live biomass (Haferkamp and MacNeil, 2004; Derner et al., 2006). In the shortgrass-steppe and mixed-grass prairie heavy grazing has been reported to increase the abundance of blue grama, at the expense of cool season grasses (e.g., western wheatgrass), the former species being effective at sequestering SOC (Frank et al., 1995; Schuman et al., 1999; Reeder and Schuman, 2002). This pattern was examined in several studies that concluded that precipitation typically has a stronger influence than grazing on overall carbon flux (Haferkamp and MacNeil, 2004; Chimner and Welker, 2011), though grazing can considerably alter species composition (Schuman et al., 1999).

The shortgrass and mixed-grass prairie possessed a negative average EPA to NEP temporal correlation (Table 1; Fig. 4). Conversely, the tallgrass prairie had more positive average temporal correlations between EPA and NEP. Several ecoregions (Central Great Plains, High Plains, and Sand Hills) had an average EPA to NEP correlation near zero (Table 1), due to a large range of correlation direction and magnitude within these ecoregions (Fig. 4). The exception to the pattern of negative EPA to NEP correlation in the shortgrass prairie was the Southwest Tablelands, which had the strongest positive correlation between EPA and NEP of any ecoregion. The average annual precipitation where the EPA to NEP correlation becomes negative is 359 mm, close to the 370–400 mm mean annual precipitation zone that represents a transition in aboveground response to grazing and rates of nutrient cycling (Sims et al., 1978). Variability of per pixel EPA to NEP correlation within each ecoregion is likely due to site biophysical conditions and grazing intensity. For example, a heavily grazed pasture in the mesic Flint Hills ecoregion may tend to have a more negative EPA to NEP relationship than the ecoregion average, and behave more similarly to the drier mixed-grass prairie.

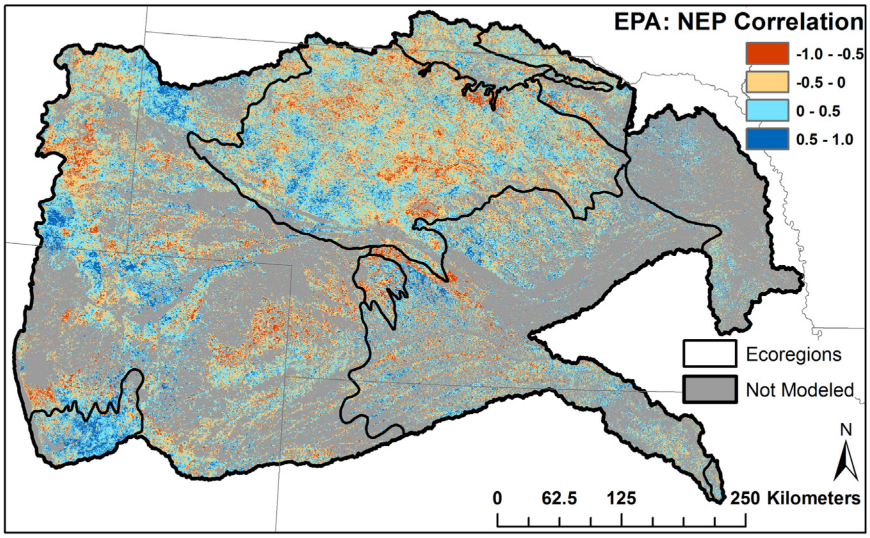

Fig. 4. Temporal correlation coefficient (r) by pixel between yearly Ecosystem Performance Anomaly (EPA) and yearly Net Ecosystem Productivity (NEP) as the dependent variable for 2000–2008 ($n = 9$ per pixel). Refer to Fig. 1C for ecoregion labels.

3.3.2. NEP phenology

Yearly NEP phenologies (in weekly time intervals), averaged across the study period, were calculated for each grassland type (Fig. 5) and ecoregion (Fig. 6). The seasonal pattern of phenology in each grassland type and ecoregion generally progressed as negative NEP in winter (Wylie et al., 2007), sharp increase in spring with ample precipitation (Sims et al., 1978; Frank and Karn, 2003), peak in early summer (usually in week 20–23) (Chimner and Welker, 2011), then decline in late summer (usually in week 25–35) frequently becoming negative with drought and precipitation deficits. This pattern is largely due to 75% of annual precipitation accumulating during the April to September period in the Great Plains (Sims et al., 1978), much of it concentrated in April to June. Other ecosystem attributes, such as above ground biomass, LAI, and carbon assimilation also often have peaks in mid-June to early-August (Frank and Karn, 2003).

The gradient of reduced average annual precipitation from the tallgrass to mixed-grass to shortgrass prairie corresponds with a pattern of dampened peak weekly NEP, shorter growing season (Fig. 5), and lower cumulative NEP along this gradient (Table 1; Svejcar et al., 2008). Peak CO_2 flux rates were reported to reach 7.8 g C m^{-2} day^{-1} in the Northern Great Plains (Frank and Karn, 2003). Our maximum rate was lower, approximately 3 g C m^{-2} day^{-1} in both the Western Corn Belt Plains and Flint Hills (Fig. 6B and F), this was due to the weekly temporal resolution of the data and averaging the NEP phenology over the study years, both of which tend to reduce extreme values.

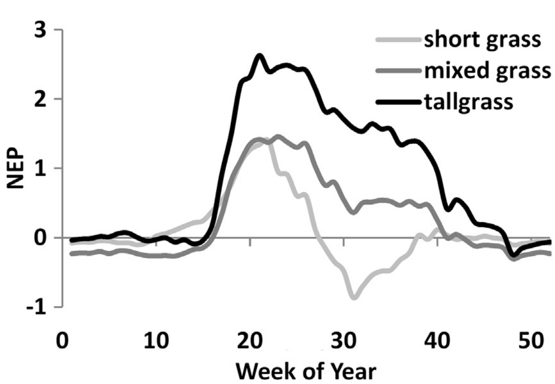

Fig. 5. Mean weekly Net Ecosystem Productivity (NEP) (g C m^{-2} day^{-1}) for the shortgrass (High Plains and Southwestern Tablelands ecoregions), mixed-grass (Nebraska Sand Hills, Northwestern Great Plains, and Northwestern Glaciated Plains), and tallgrass (Central Great Plains, Western Corn Belt Plains, and Flint Hills ecoregions) prairies in the Greater Platte River Basin for 2000–2008.

3.3.3. Impact of disturbance on NEP phenology

Mean annual precipitation is positively related to grassland carbon sequestration rates, regardless of stocking rate (Derner and Schuman, 2007). As a result, underperforming (often heavily grazed) sites in mesic ecoregions such as the Flint Hills have a higher NEP than overperforming (such as lightly grazed/ungrazed) sites in drier ecoregions such as the High Plains (Fig. 6A and F; Table 2). The impacts of management/disturbance (as represented by EPA performance classes) on NEP phenology are significant (Zhu et al., 2011), however, and vary considerably by ecoregion (Fig. 6; Table 2).

Ecoregions with stronger EPA to NEP correlations (both positive and negative) (Table 1) tend to have a greater NEP phenology difference by EPA class (Fig. 6C, D, and G), and significant differences in cumulative NEP by EPA class (Table 2), suggesting that SOC in these ecoregions is more vulnerable/sensitive to grazing and disturbance. The High Plains ecoregion is an outlier to this pattern, with a weak negative EPA to NEP correlation and a large difference in NEP among EPA performance classes (Fig. 6A; Table 2). The

Table 2
Mean yearly cumulative Net Ecosystem Productivity (NEP; g C m^{-2} yr^{-1}) by Ecosystem Performance Anomaly (EPA) classes (underperforming, normal performing and overperforming) within each ecoregion for 2000–2008 in grasslands of the Greater Platte River Basin (corresponding with the plots in Fig. 6). Letters indicate a significant difference ($P < 0.05$) within a row. Carbon uptake is denoted by a positive NEP and release to the atmosphere as a negative value.

Ecoregion	EPA class		
	Under	Normal	Over
High Plains	−4.2a	3.7b	18.9c
Western Corn Belt Plains	39.6a	41.7a	44.2a
Nebraska Sand Hills	−1.6a	3.5b	15.1c
Northwestern Great Plains	19.4a	29.7b	31.6b
Northwestern Glaciated Plains	33.1a	33.3a	33.0a
Flint Hills	49.1a	47.9a	46.5a
Southwest Tablelands	−9.4a	6.5b	23.5c
Central Great Plains	38.4a	45.1b	45.4b
Study Area Average	10.4a	16.6b	24.8c

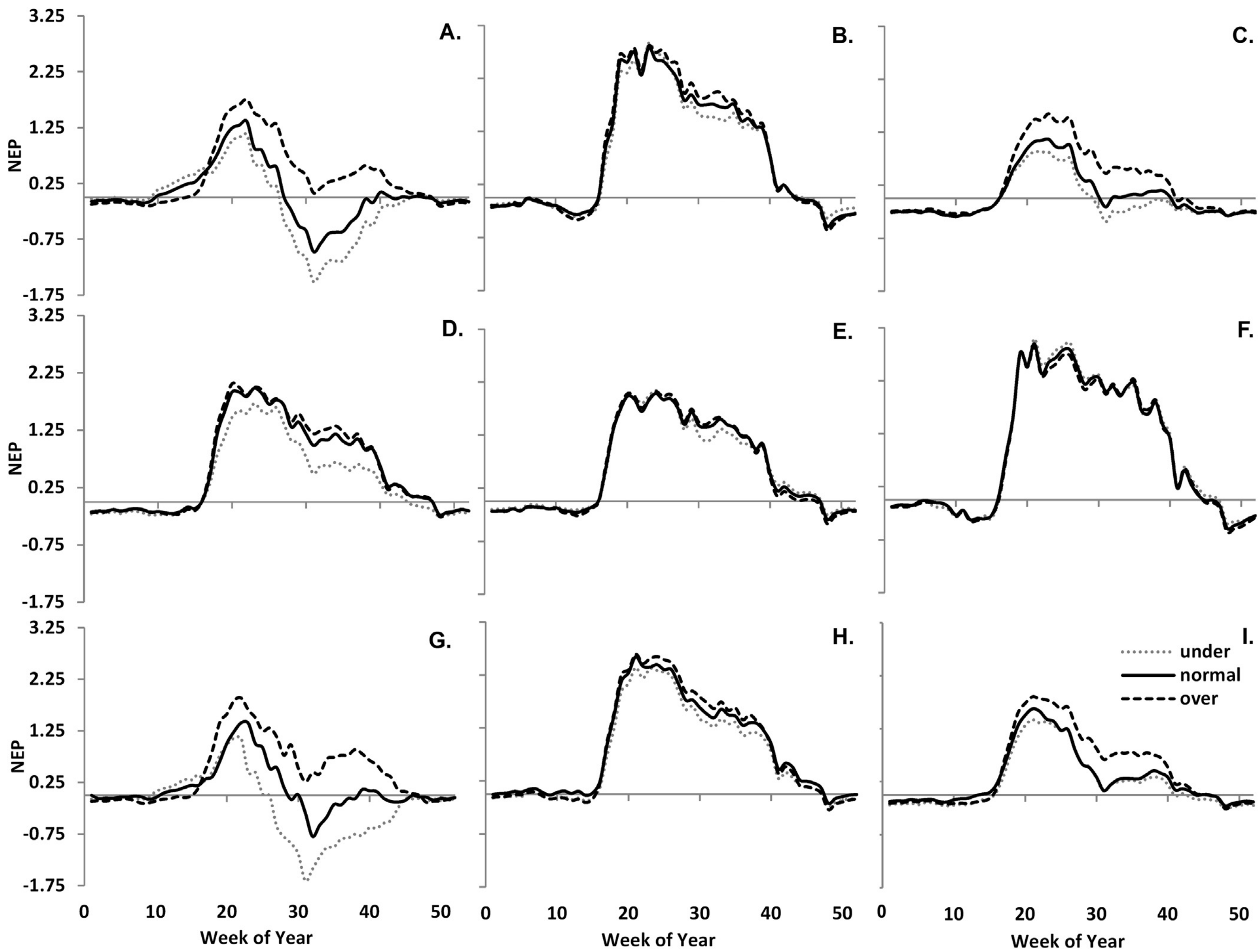

Fig. 6. 2000–2008 average weekly NEP ($g\,C\,m^{-2}\,day^{-1}$) by Ecosystem Performance Anomaly (EPA) classes (underperforming, normal performing, and over performing) in the (A) High Plains, (B) Western Corn Belt Plains, (C) Nebraska Sand Hills, (D) Northwestern Great Plains, (E) Northwestern Glaciated Plains, (F) Flint Hills, (G) Southwest Tablelands, (H) Central Great Plains ecoregions, and (I) overall average.

Flint Hills is also an outlier to this pattern with a relatively strong positive correlation between EPA and NEP, but little difference in NEP phenology by EPA class. Another driver of differences in NEP phenology and cumulative NEP among EPA classes was average annual precipitation; ecoregions with greater average annual precipitation tended to have smaller differences in NEP phenology by EPA class (Fig. 6B, E, F, and H) than those with less precipitation (Fig. 6A, C, D, and G; Table 2).

We found weak negative correlations between EPA and NEP in portions of the shortgrass and mixed-grass prairie (Table 1), in agreement with previous work (Milchunas and Lauenroth, 1993; Chimner and Welker, 2011). However, our data show that underperforming areas in the shortgrass (Fig. 6A and G) and mixed-grass (Fig. 6C, D, E, and H) ecoregions have a lower NEP throughout much of the growing season, as compared to the overperforming areas. Instances in which underperforming areas have a higher NEP than overperforming ones are limited to several weeks in the beginning of the growing season (in the High Plains, Southwest Tablelands, and Central Great Plains), likely due to less litter cover in underperforming sites. Additionally, the midsummer peak NEP in the Flint Hills is higher in underperforming sites, presumably because fire is frequently used as a management practice in the ecoregion, and growth may be enhanced following the fires (Blair, 1997). In no case, however, is the cumulative yearly NEP for underperforming sites in an ecoregion significantly higher than overperforming sites (Table 2). Although some ecoregions (e.g., Northwest Great Plains and High Plains) have a negative average EPA to NEP correlation (i.e., disturbance increases NEP; Table 1), the overperforming sites in these ecoregions have a higher average NEP than normal and underperforming sites (Table 2; Fig. 6). This discrepancy results from the frequency of EPA values; most pixels in each ecoregion are 'normal' performing.

Most ecoregions follow the expected positive relationship between EPA and NEP (i.e., disturbance reduces NEP) during the majority of the growing season. As such, overperforming sites among all ecoregions had higher NEP than the corresponding underperforming sites in 66.3% of weekly periods throughout the year, and in 86.9% of growing season (April to September) weeks (Fig. 6). The greatest differences in NEP among EPA classes, when evident, tended to occur in late summer (usually week 25–40; Fig. 6). This pattern may be due the frequent precipitation deficits during this period of the year. Differences in rates of CO_2 flux among grazed, ungrazed prairie, and shrub prairie sites in the Northern Great Plains, for example, were greater in a drought year, compared to non-drought years, and grazed prairie tended to have a lower rate of CO_2 flux than a similar ungrazed prairie (Frank and Karn, 2003). The timing of grazing is important; grazing in the dry summer months (when plants are frequently under moisture stress) often results in little to no regrowth. Short-term intensive grazing in May, for example, reduced live biomass in the 60 subsequent days and reduced CO_2 flux for 30 days, while grazing in July reduced live biomass in the 90 subsequent days (Haferkamp and MacNeil, 2004).

Adjusting stocking rates, adding cattle watering facilities to improve utilization, inter-seeding alfalfa, burning, fertilizing, and grassland restoration have all been cited as management actions that could promote carbon sequestration (Campbell et al., 2004; Ritten et al., 2012). Generally, practices that reduce soil erosion and increase grassland productivity will also increase carbon sequestration rates and the sustainable livestock carrying capacity (Campbell et al., 2004). In ecoregions with little difference in NEP among EPA classes, management may be relatively less important than climatic drivers, or the diversity of management (grazing) impacts may be low. Conversely, in the shortgrass prairie, where NEP is very sensitive to grazing/disturbance, minimizing SOC losses might be a more effective management objective than gaining SOC (Schuman et al., 2002).

Zhu et al. (2011) reported that grazing (assuming moderate intensity) in Great Plains grasslands removed 107 Tg C yr^{-1}, or 15% of the annual carbon sink, while Frank et al. (1995) found 17% less SOC in moderately grazed pastures compared to grazing exclosures in the mixed-grass prairie. Our data suggest a stronger grazing/disturbance impact, with the average NEP at normal performing and underperforming sites 33% and 58% lower than overperforming sites (Table 2). If proper grazing intensity can increase carbon storage on grasslands by 10–30 g m^{-2} yr^{-1} as suggested by Schuman et al. (2002), a significant (additional) portion of the study area could attain a NEP greater or equal to zero with improved management; 30% of the grassland area assuming a 30 g m^{-2} yr^{-1} increase is possible with improved management, and 12% assuming a 10 g m^{-2} yr^{-1} increase due to management.

4. Conclusions

Grazing/disturbance had a moderately strong influence on NEP phenology and cumulative NEP; however, climate and biophysical conditions were usually more important. The NEP response to disturbance varies by ecoregion, and more generally by grassland type, where the shortgrass prairie NEP is most responsive to disturbance, the mixed-grass prairie displays a moderate response, and tallgrass prairie is the least impacted by disturbance. Most areas demonstrated the expected positive correlation between disturbance (EPA) and NEP. Notable exceptions to this pattern were (1) higher NEP in underperforming sites than overperforming sites near the start of growing season [in shortgrass prairie], and (2) the Flint Hills ecoregion, where underperforming sites had a higher cumulative NEP than overperforming sites.

The PD values of grasslands describe the difference between actual average annual precipitation and that required to sustain a carbon sink. This information could be useful in assessing the capability of management to influence carbon balance. Areas of positive NEP and positive PD for example, are likely relatively stable and would likely require the combination of a drought and heavy grazing to induce a negative NEP. Conversely, regions with a negative PD and negative NEP would require extensive management intervention to achieve a carbon balance. Regions with positive or neutral PD (and a negative 2000–2008 average NEP) in the shortgrass and mixed-grass prairies may constitute the best opportunity for land management practices to sequester additional carbon, because of the greatest difference in cumulative NEP among EPA classes in these areas and probable lack of SOC equilibrium. Tallgrass prairie has a much greater potential to assimilate carbon, however, and its restoration would provide a greater net carbon sink per unit area.

The difficult task of managing grasslands (e.g., grazing) appropriately to site conditions is made even more difficult with the consideration of carbon flux. As previously discussed, no simple relationship exists between grazing pressure and carbon flux. Moreover, management actions that increase carbon sequestration do not always promote overall ecosystem health or livestock production (Reeder and Schuman, 2002). Overall, light to moderate stocking rates have been generally associated with greater ecosystem goods and services compared to either heavy grazing or exclusion from grazing. Sustainable management practices in the tallgrass and wetter portions of the mixed-grass prairie should induce a long-term average net carbon sink, in the shortgrass prairie and drier portions of the mixed-grass prairie, however, management should typically be considered sustainable if equilibrium SOC is simply maintained.

Acknowledgments

Research was funded by the USGS Climate and Land Use Research and Development Program, USGS Land Change Science, USGS Climate Effects Network, and USGS GD Biofuels Program. We acknowledge the Ameriflux network and the USDA Agriflux network for providing flux tower data. We also thank Norman Bliss, Larry Tieszen, Gregg Johnson, and two anonymous reviews for their insightful comments.

References

Blair, J.M., 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78, 2259–2368.

Campbell, S., Mooney, S., Hewlett, J.P., Menkhaus, D.J., Vance, G.F., 2004. Can ranchers slow climate change? Rangelands 26, 16–22.

Chapin, F.S. III, Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R., Wirth, C., Aber, J.D., Cole, J.J., Goulden, M.L., Harden, J.W., Heimann, M., Howarth, R.W., Matson, P.A., McGuire, A.D., Melillo, J.M., Mooney, H.A., Neff, J.C., Houghton, R.A., Pace, M.L., Ryan, M.G., Running, S.W., Sala, O.E., Schlesinger, W.H., Schulze, E.D., 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9, 1041–1050.

Chimner, R.A., Welker, J.M., 2011. Influence of grazing and precipitation on ecosystem carbon cycling in a mixed-grass prairie. Pastoralism: Res. Policy Pract. 1, 20.

Derner, J.D., Boutton, T.W., Briske, D.D., 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant Soil 280, 77–90.

Derner, J.D., Schuman, G.E., 2007. Carbon sequestration and rangelands: a synthesis of land management and precipitation effects. J. Soil Water Conserv. 62, 77–85.

Frank, A.B., Tanaka, L., Hofmann, L., Follett, R.F., 1995. Soil carbon and nitrogen of the Northern Great Plains grasslands as influenced by long-term grazing. J. Range Manage. 48, 470–474.

Frank, A.B., Karn, J.F., 2003. Vegetation indices, CO_2 flux, and biomass for northern plains grasslands. J. Range Manage. 56, 382–387.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 national land cover database for the conterminous United States. Photogramm. Eng. Rem. S. 77, 858–864.

Gebhart, D.L., Johnson, H.S., Mayeux, H.S., Polley, H.W., 1994. The CRP increases soil organic carbon. J. Soil Water Conserv. 49, 488–492.

Gilmanov, T.G., Tieszen, L.L., Wylie, B.K., Flanagan, L.B., Frank, A.B., Haferkamp, M.R., Meyers, T.P., Morgan, J.A., 2005. Integration of CO_2 flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. Global Ecol. Biogeogr. 14, 271–292.

Gu, Y., Wylie, B.K., Zhang, L., Gilmanov, T.G., 2012. Evaluation of carbon fluxes and trends (2000–2008) in the Greater Platte River Basin: A sustainability study for potential biofuel feedstock development. Biomass Bioenerg. 47, 145–152.

Gu, Y., Wylie, B.K., Bliss, N.B., 2013. Mapping grassland productivity with 250-m eMODIS NDVI and SSURGO over the Greater Platte River Basin, USA. Ecol. Indic. 24, 31–36.

Haferkamp, M.R., MacNeil, M.D., 2004. Grazing effects on carbon dynamics in the northern mixed-grass prairie. Environ. Manage. 33, s462–s474.

Jenkerson, C.B., Maiersperger, T.K., Schmidt, G.L., 2010. eMODIS: a user-friendly data source. U.S. Geologic Survey Open File Report, 2010–1055, p. 10.

Johnson, J.R., Larson, G.E., 2007. Grassland Plants of South Dakota and the Northern Great Plains, vol. B-566 rev. South Dakota State University, South Dakota Agricultural Experiment Station, Brookings, SD, USA, pp. 288.

Law, B.E., 2007. AmeriFlux network aids global synthesis. EOS T. Am. Geophys. Un. 88, 286.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 64, 327–366.
Meyers, T.P., 2001. A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions. Agr. Forest Meteorol. 106, 205–214.
Omernik, J.M., 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. 77, 118–125.
Owensby, C.E., Ham, J.M., Auen, L.M., 2006. Fluxes of CO_2 from grazed and ungrazed tallgrass prairie. Rangeland Ecol. Manage. 59, 111–127.
Randerson, J.T., Chapin, F.S. III, Harden, J.W., Neff, J.C., Harmon, M.E., 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. Ecol. Appl. 12, 937–947.
Reeder, J.D., Schuman, G.E., 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environ. Pollut. 116, 457–463.
Rigge, M., Wylie, B.K., Gu, Y., Belnap, J., Phuyal, K., Tieszen, L.L., 2013. Monitoring the status of forests and rangelands in the western United States using ecosystem performance anomalies. Int. J. Remote Sens. 34, 4049–4068.
Ritten, J.P., Bastian, C.T., Rashford, B.S., 2012. Profitability of carbon sequestration in western rangelands of the United States. Rangeland Ecol.Manage. 65, 340–350.
Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A., 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9, 65–71.
Schuman, G.E., Janzen, H.H., Herrick, J.E., 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environ. Pollut. 116, 391–396.
Sims, P.L., Singh, J.S., Lauenroth, W.K., 1978. The structure and function of ten western North American grasslands I. Abiotic and vegetational characteristics. J. Ecol. 66, 251–285.
Soussana, J.-F., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., Arrouays, D., 2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use Manage. 20, 219–230.
Svejcar, T., Mayeux, H., Angell, R., 1997. The rangeland carbon dioxide flux project. Rangelands 19, 16–18.
Svejcar, T., Angell, R., Bradford, J.A., Dugas, W., Emmerich, W., Frank, A.B., Gilmanov, T.G., Haferkamp, M., Johnson, D.A., Mayeux, H., Mielnick, P., Morgan, J., Saliendra, N.Z., Schuman, G.E., Sims, P.L., Snyder, K., 2008. Carbon fluxes on North American rangelands. Rangeland Ecol. Manage. 61, 465–474.
Swets, D.L., Reed, B.C., Rowland, J.R., Marko, S.E., 2000. A weighted least squares approach to temporal NDVI smoothing. In: Paper presented at American Society of Photogrammetric Remote Sensing 1999, Portland, OR, USA.
Tieszen, L.L., Reed, B.C., Bliss, N.B., Wylie, B.K., DeJong, D.D., 1997. NDVI, C_3 and C_4 production, and distributions in Great Plains grassland land cover classes. Ecol. Appl. 7, 59–78.
Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.
Wylie, B.K., Fosnight, E.A., Gilmanov, T.G., Frank, A.B., Morgan, J.A., Haferkamp, M.R., Meyers, T.P., 2007. Adaptive data-driven models for estimating carbon fluxes in the northern Great Plains. Remote Sens. Environ. 106, 399–413.
Wylie, B.K., Zhang, L., Ji, L., Tieszen, L.L., Jolly, M., 2008. Integrating modeling and remote sensing to identify ecosystem performance anomalies in the boreal forest, Yukon River Basin, Alaska. Int. J. Dig. Earth 1, 196–220.
Zhang, L., Wylie, B., Loveland, T., Fosnight, E., Tieszen, L., Ji, L., Gilmanov, T.G., 2007. Evaluation and comparison of gross primary production estimates for the Northern Great Plains grasslands. Remote Sens. Environ. 106, 173–189.
Zhang, L., Wylie, B., Ji, L., Gilmanov, T.G., Tieszen, L., 2010. Climate-driven interannual variability in net ecosystem exchange in the northern Great Plains grasslands. Rangeland Ecol.Manage. 63, 40–50.
Zhang, L., Wylie, B.K., Ji, L., Gilmanov, T.G., Tieszen, L.L., Howard, D.M., 2011. Upscaling carbon fluxes over the Great Plains grasslands: sinks and sources. J. Geophys. Res. 116, G00J03.
Zhu, Z. (Ed.), Bouchard, M., Butman, D., Hawbaker, T., Li, Z., Liu, J., Liu, S., McDonald, C., Reker, R., Sayler, K., Sleeter, B., Sohl, T., Stackpoole, S., Wein, A., Zhu, Z., 2011. Baseline and projected future carbon storage and greenhouse-gas fluxes in the Great Plains region of the United States. U.S. Geological Survey Professional Paper 1787, p. 28.